# Magnetotactic Bacteria

## INTRODUCTION

Although life has evolved in it, the geomagnetic field has generally not been accorded a role in the lives of organisms other than humans. However, over the last twenty years evidence has accumulated that certain species as diverse as homing pigeons,[1] bees,[2] salamanders,[3] skates,[4] mice[5] and perhaps humans[6,7] can use the geomagnetic fields as a behavioral cue under certain circumstances. However, the most convincing demonstration of magnetic field sensitivity occurs in certain bacteria from aquatic sediments that orient and swim in a preferred direction in homogeneous magnetic fields of the order of and including the geomagnetic field (~0.5 G).[8] This behavior is termed magnetotaxis.

Magnetotactic bacteria were discovered serendipitously in the early 1970's by Richard P. Blakemore.[8] He found various morphological types of magnetically sensitive bacteria in both freshwater and marine muds, indicating that the phenomenon is spread over various species. Blakemore and Kalmijn[9] used homogeneous magnetic fields produced by Helmholtz coils to show that New England bacteria swim along magnetic field lines in the field direction, that is, in the direction indicated by the North-seeking end of a magnetic compass needle. When the field produced by the coils is reversed by reversing the direction of current flow, the bacteria respond immediately by executing U-turns and continuing to swim in the field direction. Killed cells orient along the field lines and rotate when the field direction is reversed, but do not move

along the field lines. Thus, magnetotactic bacteria from New England behave as magnetic dipoles and are predominently North-seeking.

## MECHANISM

All magnetotactic bacteria examined to date contain magnetosomes,[10] which are unique, intracytoplasmic structures consisting of enveloped $Fe_3O_4$ particles (Figure 1).[11,12] One species, *Aquaspirillum magnetotacticum* has been isolated and grown in pure culture in a chemically defined medium.[13] In this species there are typically 20–25 cuboidal $Fe_3O_4$ particles about 500 Å on a side, per cell.[11] The particles are arranged in a chain which is fixed along the axis of motility of the bacterium. Magnetosomes are arranged in one or two chains in most other species as well. Since only soluble ferric iron is available in the growth medium, the presence of intracytoplasmic $Fe_3O_4$ in *A. magnetotacticum* implies a bacterial biomineralization process. In fact, since total cellular iron is about 2% of the cellular dry weight, these bacteria

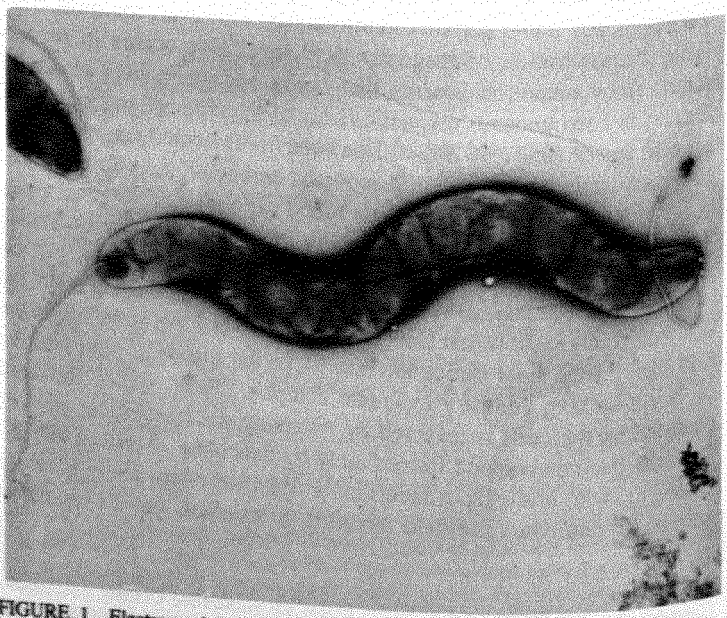

FIGURE 1 Electron micrograph of a magnetotactic bacterium. The electron opaque particles are the magnetosomes, the enveloped $Fe_3O_4$ particles.

are prodigious manufacturers of $Fe_3O_4$. If iron is withheld from the growth medium, bacteria grow without magnetosomes[13]; these cells are nonmagnetotactic. Thus the magnetotactic response is definitely correlated with the presence of the magnetosomes.

$Fe_3O_4$ is ferrimagnetic with a Curie temperature of 580°C.[14] $Fe_3O_4$ particles of 500 Å dimensions are single magnetic domains with a permanent magnetic moment approaching the saturation magnetization of bulk $Fe_3O_4$, 480 G/cm$^3$. Larger ferrimagnetic particles form magnetic domains, reducing the magnetostatic energy and the remanent magnetic moment. The upper size limit for single magnetic domains is approximately the width of a domain wall $d_w$, which is a function of the exchange and anisotropy energy of the material:

$$d_w \simeq \left(\frac{kT_c}{Ka^3}\right)^{1/2} a, \tag{1}$$

where $k$ is the Boltzman constant, $T_c$ the Curie temperature, $K$ the anisotropy energy and $a$ the atomic spacing. Substituting values for $Fe_3O_4$ yields

$$d_w \sim \left(\frac{10^{-13}}{10^{+5} \times 10^{-22}}\right)^{1/2} \times 5 \times 10^{-8} \text{ cm} \sim 500 \text{ Å}.$$

More precise calculations by Butler and Banerjee[15] for cubic particles yield $d_w \simeq 760$ Å. On the other hand, if the particle dimension is less than a certain value $d_s$, it will be superparamagnetic at room temperature, that is, thermal energy will excite transitions of the magnetic moment between equivalent easy magnetic axes of the particle with a consequent loss of the time-averaged remanent moment.[16] The transition probability is a function of the anisotropy energy and the thermal energy:

$$\tau \sim \tau_0 \exp[KV/2kT], \tag{2}$$

where $\tau_0$ is a constant of the order of $10^{-9}$ s and $V(=d_s)$ is the particle volume. Particles of dimensions greater than 350 Å are stable for times greater than $10^6$ years; hence $d_s < 350$ Å. Thus particles of $Fe_3O_4$ with dimensions 350 Å $< d <$ 760 Å are permanent, single magnetic domains with remanent moments of 480 G/cc. So we can assume that each 500 Å particle produced by a bacterium has a moment of $6.0 \times 10^{-14}$ emu.

When the single domain particles are organized in a chain as they are in *A. magnetotacticum*, the interactions between the particle mo-

ments will cause them to be oriented parallel to each other along the chain direction.[17] Thus the moment of the entire chain will be equal to the sum of the individual particle moments. For chains of 22 particles, this gives a total remanent moment $M = 1.3 \times 10^{-12}$ emu. Since the particles are fixed in the bacterium by the magnetosome envelope[10] the bacterium is, in effect, a swimming magnetic dipole.

The simplest hypothesis for magnetotaxis is passive orientation of the swimming bacterium along the magnetic field lines by the torque exerted by the field on the magnetic moment.[18] Thermal energy, on the other hand, will tend to disorient the bacterium during swimming. The energy of the bacterial moment in a magnetic field $H$ is given by

$$\begin{aligned} E_m &= -\mathbf{M} \cdot \mathbf{H} \\ &= -MH \cos \theta, \end{aligned} \tag{3}$$

where $\theta$ is the angle between $M$ and $H$. The thermally averaged orientation of an ensemble of moments, or equivalently, the time averaged orientation of a single moment, is written

$$\begin{aligned} \langle \cos \theta \rangle &= \frac{\int \cos \theta \, e^{E_m/kT} \, dV}{\int e^{-E_m/kT} \, dV} \\ &= L(\alpha); \qquad \alpha = MH/kT. \end{aligned} \tag{4}$$

$L(\alpha)$ is the Langevin function:

$$L(\alpha) = \coth(\alpha) - 1/\alpha, \tag{5}$$

and is plotted in Figure 2. If we consider *A. magnetotacticum* in the earth's magnetic field of 0.5 G at room temperature, $\alpha \sim 16$ and $\langle \cos \theta \rangle > 0.9$. Because the Langevin function asymptotically approaches 1 as $\alpha$ increases, the orientation would not significantly improve if there were more particles and the moment per bacterium were larger. Thus each bacterium is in effect a biomagnetic compass optimized to the geomagnetic field at room temperature.

The migration velocity along the magnetic field lines

$$v_H = v_0 \langle \cos \theta \rangle, \tag{6}$$

where $v_0$ is the forward velocity of the swimming bacterium and $\theta$ is the angle between the axis of motility and the magnetic field. If $v_0$ is independent of $H$ and the magnetic moment is parallel to the axis of motility,

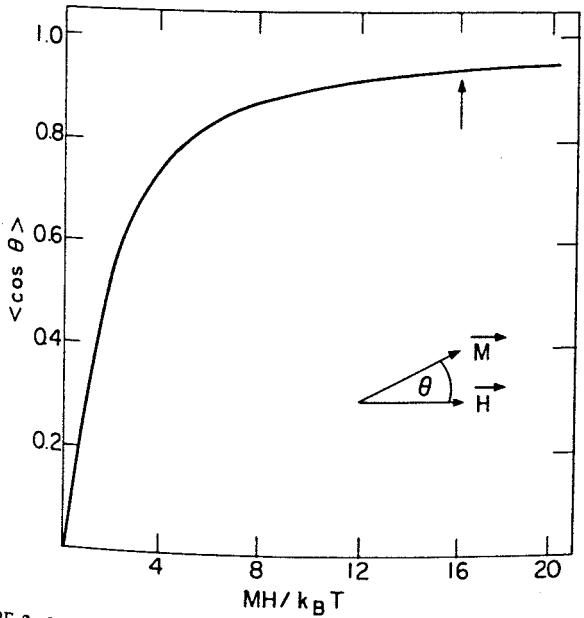


FIGURE 2 Langevin function plotted as a function of $MH/kT$. The arrow indicates the average orientation of bacteria containing 22 500-Å particles of $Fe_3O_4$ in the geomagnetic field of 0.5 G at room temperature.

$$v_H = v_0 L(\alpha), \tag{7}$$

providing that the velocity is averaged over a time which is long compared to the rotational diffusion time,

$$\tau \simeq 8\pi r^3 \eta / kT \simeq 1 \text{ s}, \tag{8}$$

where $r$ is the effective hydrodynamic radius of the bacterium $\simeq 0.5$ μm and $\eta$ is the viscosity of water $\simeq 0.01$ poise. For bacteria with moments $> 10^{-12}$ emu, the migration speed along magnetic field lines is thus $> 90\%$ of their forward speed. This may be compared with migration speeds of the order of 10% of the forward speed in chemotaxis, the response by which certain bacteria swim up or down chemical concentration gradients.[19]

The magnetic moments of bacteria can be calculated from measurements of migration velocities $v_H$ as a function of magnetic field strength, and fitting the results with Eq. (7). This method was first applied to groups of bacteria from sediments,[20] and subsequently to single bac-

teria.[21,22] The results are consistent with the moment calculated by estimating the volume of $Fe_3O_4$ from electron micrographs. Because the moments in a group of bacteria will be distributed about the mean value $\langle M \rangle$, the method for groups of bacteria will be valid only in the limit of large $\alpha$ ($\alpha > 10$) where $L(\alpha) \rightarrow (1 - 1/\alpha)$, and if the width of the distribution is narrow.

The magnetic moment per cell could also be determined from the width of a U-turn executed by a bacterium following field reversal.[23,24] The discussion here follows the derivation by C. P. Bean.[24] In the world of the bacterium, inertial effects are negligible[25] and hence the torque exerted on the moment by the field is proportional to angular velocity:

$$\mathbf{M} \times \mathbf{H} = MH \sin \theta = 8\pi r^3 \eta \frac{d\theta}{dt}. \tag{9}$$

We define

$$\tau_0 = \frac{8\pi r^3 \eta}{MH}; \tag{10}$$

then the velocity perpendicular to the field

$$\begin{aligned} v_\perp &= v_0 \sin \theta \\ &= v_0 \tau_0 \frac{d\theta}{dt}. \end{aligned} \tag{11}$$

The width of the U-turn

$$\begin{aligned} W &= \int v_\perp \, dt \\ &= v_0 \tau_0 \pi. \end{aligned} \tag{12}$$

From the definition of $\tau_0$, $W$ is inversely proportional to $MH$ and a measurement of $W$ can in principle yield $M$. An actual measurement, however, is complicated by the requirement that the bacterium be confined to a horizontal plane during the U-turn. It is also possible in principle to use magnetic measurements to obtain the average moment of the population and the mean squared deviation. If $P(M)$ is the probability distribution for $M$,

$$\int P(M) \, dM = 1, \tag{13}$$

and

$$\langle M \rangle = \int P(M) \, M \, dM. \tag{14}$$

The magnetization of a sample is written

$$M_H = NV \int P(M)\, M\, L\,(\alpha)\, dM, \tag{15}$$

where $N$ is the number of bacteria per cc and $V$ is the sample volume. In the limit of large $\alpha$, $L(\alpha) \to 1 - 1/\alpha$ and

$$M_H = NV \int P(M) M \left(1 - \frac{kT}{MH}\right) dM \tag{16}$$

$$= NV\langle M\rangle \left(1 - \frac{kT}{\langle M\rangle H}\right). \tag{17}$$

As $H$ increases the term in brackets approaches 1 and

$$M_H \to NV\langle M\rangle. \tag{18}$$

In the limit of $\alpha \to 0$, $L(\alpha) \to \alpha/3$ and

$$M_H = NV \int P(M) M \cdot \frac{MH}{3kT}\, dM \tag{19}$$

$$= NV \frac{\langle M^2\rangle H}{3kT}.$$

The mean squared deviation is by definition

$$\delta^2 = \langle M^2\rangle - \langle M\rangle^2. \tag{20}$$

Hence, measurement of the saturation moment of the sample and the initial slope can give a measure of $\delta^2$. However, high measurement sensitivity is required because if $M = 10^{-12}$ emu and $N = 10^7$/cc, the saturation moment of a 1 cc sample will only be $10^{-5}$ emu. Finally, the average magnetic moment of a population can also be determined by elastic light scattering.[26] In this method, a laser beam is passed through a sample of bacteria in water in a magnetic field (Figure 3). The light




FIGURE 3 Schematic representation of light scattering experiment (see Ref. 27).

scattered at angle θ with respect to the beam is measured as a function of magnetic field strength. If we define the scattering vector $\mathbf{Q} = \mathbf{k}_f - \mathbf{k}_i$ where $\mathbf{k}_f$ and $\mathbf{k}_i$ are the final and initial photon momenta, and since $|k_f| = |k_i|$,

$$|Q| = 2|k| \sin(\theta/2). \tag{21}$$

The intensity of scattered light at θ is given by

$$I(\theta) \propto S(\mathbf{Q},\mathbf{H}), \tag{22}$$

where $S(\mathbf{Q},\mathbf{H})$ is the static structure factor. For small values of $\mathbf{Q}$ (parallel to $\mathbf{H}$)

$$S(\mathbf{Q},\mathbf{H}) = N \int P(\alpha,\phi) \left[ \frac{\sin(QL\cos\phi/2)}{(QL/2)\cos\phi} \right]^2 d\phi, \tag{23}$$

where $N$ is the number of scatterers, $L$ is the length of a bacterium, and $\phi$ is the angle between $\mathbf{Q}$ and the length of the bacterium. $P$ is the angular distribution function of bacteria about the $\mathbf{Q}$ and $\mathbf{H}$ axis:

$$P(\alpha,\phi) = \frac{\alpha e^{\alpha\cos\theta} \sin\phi}{2\sinh\alpha}. \tag{24}$$

Since the scattered light intensity depends on α it can be used to measure $M$. A recent application of this method to *A. magnetotacticum*[27] gives results for $M$ which are consistent with estimations of average particle size and number from electron micrographs.

Another optical method for determining the average magnetic moment of a population utilizes the magnetically induced birefringence (MIB), and depends on the polarization anisotrophy of the bacteria[27] (Figure 4). In zero magnetic field the bacteria are oriented at random and the total birefringence of the sample is zero. In an applied field the orientation distribution becomes peaked in the field direction and the birefringence of the sample increases:

$$\Delta n(H) = \Delta n_0 \left[ 1 - \frac{3\coth\alpha}{\alpha} + \frac{3}{\alpha^2} \right], \tag{25}$$

where $\Delta n_0$ is the birefringence of the sample when fully oriented at high field, and α is defined above. Determination of $\Delta n(H)$ as a function of $H$ can be fit with Eq. (25) to yield $M$. Measurements made on a

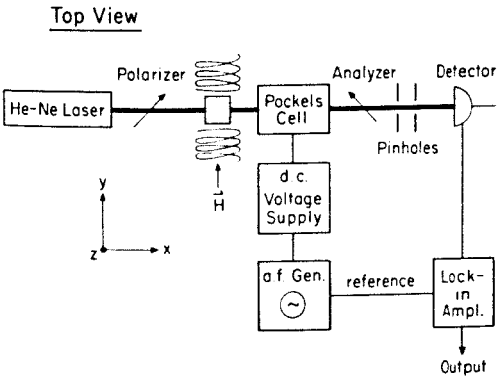


FIGURE 4 Schematic representation of magnetically induced birefringence experiment (see Ref. 27).

particular culture sample provided by R. P. Blakemore are shown in Figure 5. For this sample, $M = 1.4 \times 10^{-13}$ emu. This relatively small moment compared to other cultured samples correlates with fewer magnetosomes and indicates that the magnetic moment per bacterium is variable and depends on the conditions of growth.

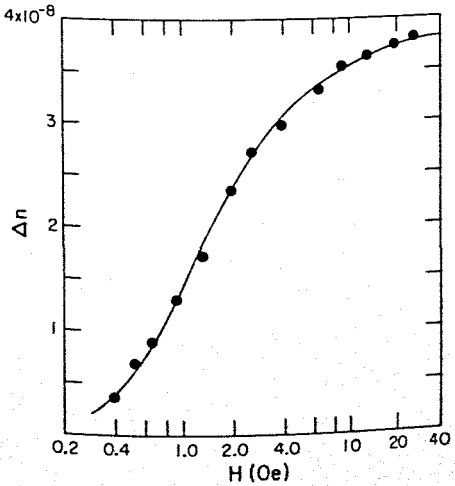


FIGURE 5 Magnetically induced birefringence of a sample of magnetotactic bacteria. The curve is a least-squares fit of the data to Eq. (25).

*A. magnetotacticum* is bipolarly flagellated, that is, it has a flagellum at both ends of the cell and can swim in either direction along the magnetic field lines. However, many other magnetotactic bacterial species one observes in sediments are asymmetrically flagellated and have unidirectional motility. As noted above, these bacteria from New England swim along magnetic field lines in the field direction. Based on the passive orientation hypothesis, this occurs if the bacterial moment is oriented in the cell forward with respect to the flagellum (Figure 6). Then the bacterium will propel itself in the field direction when the moment is oriented in the field, and will be North-seeking in the geomagnetic field. If the bacterial moment were oriented in the cell rearward with respect to the flagellum, the cell would propel itself opposite to the field direction when the moment was oriented in the field, and hence would be South-seeking in the geomagnetic field.

South-seeking bacteria have been produced in the laboratory by subjecting them to magnetic pulses[9] or ac magnetic fields[28] which are strong enough to overcome the magnetic interaction forces between the particles in the chain and cause their moments to rotate and reorient along the chain in the opposite direction. Field strengths of several hundred gauss are required,[9] consistent with magnetic measurements on freeze dried cells[20] and in agreement with estimates based on the "chain of spheres" model of Jacobs and Bean,[17] who considered the magnetic

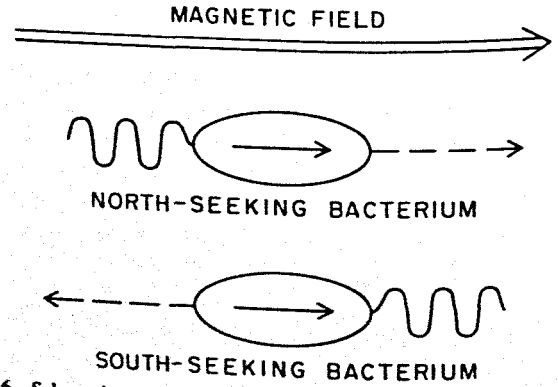


FIGURE 6 Schematic representation of North-seeking and South-seeking bacteria in an external magnetic field. The solid arrows represent the biomagnetic compasses in the bacteria, aligned along the field direction. The dashed arrows represent the respective swimming directions.

properties of a chain of single domain particles in a different context before the discovery of magnetotactic bacteria. The fact that South-seeking bacteria can be produced in the laboratory and even remagnetized back to North-seeking again leads to the question of why bacteria in New England are exclusively North-seeking, and to the larger question of what advantage is conferred by magnetotaxis on bacteria.

## BIOLOGICAL ADVANTAGE

Since many sediment-dwelling bacteria are anaerobic or microaerophilic, it would be advantageous for them to have mechanisms that prevent them from swimming up toward the toxic, higher oxygen concentration at the water surface, and keep them in the sediments. Magnetotaxis serves this purpose. Since the geomagnetic field is approximately dipolar the magnetic field lines at the earth's surface are inclined at an angle that increases with latitude. The total field intensity at latitude $\theta$ is approximately

$$H_G = 0.3\ (3 \sin^2 \theta + 1)^{1/2}\ G, \tag{26}$$

and the inclination $I$ from the horizontal is given by

$$\tan I = 2 \tan \theta. \tag{27}$$

In the Northern Hemisphere the field is inclined downwards, pointing straight down at the North magnetic pole. In the Southern Hemisphere the field is inclined upwards, at an angle increasing with latitude, pointing straight up at the South magnetic pole. At the geomagnetic equator the field is horizontal. Because of the inclination of the field lines, North-seeking bacteria migrate downward in the North Hemisphere and upward in the Southern Hemisphere (Figure 7). South-seeking bacteria migrate upward in the Northern Hemisphere and downward in the Southern Hemisphere. At the equator, both polarity types migrate horizontally. If downward directed motion is advantageous, North-seeking bacteria would be favored in the Southern Hemisphere. At the equator neither polarity would be favored.

Examination of bacteria in sediments from various places in the world confirms this hypothesis (Figure 8). In contrast to New England[8] (inclination 70°N) and other Northern Hemisphere locales,[30] magnetotactic bacteria in fresh water and marine sediments in Australia and New

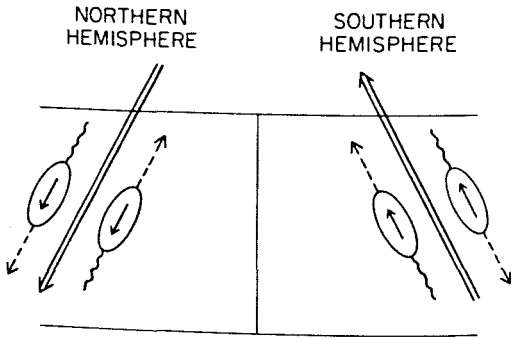


FIGURE 7 Swimming directions of North-seeking and South-seeking bacteria in the downward-inclined and upward-inclined geomagnetic field in the Northern and Southern Hemispheres, respectively.

Zealand (inclination 70°S) are almost exclusively South-seeking.[28,31] These bacteria have chains of particles and can be remagnetized to North-seeking polarity. At the geomagnetic equator in Brazil (inclination 0°) both North-seeking and South-seeking bacteria are present in

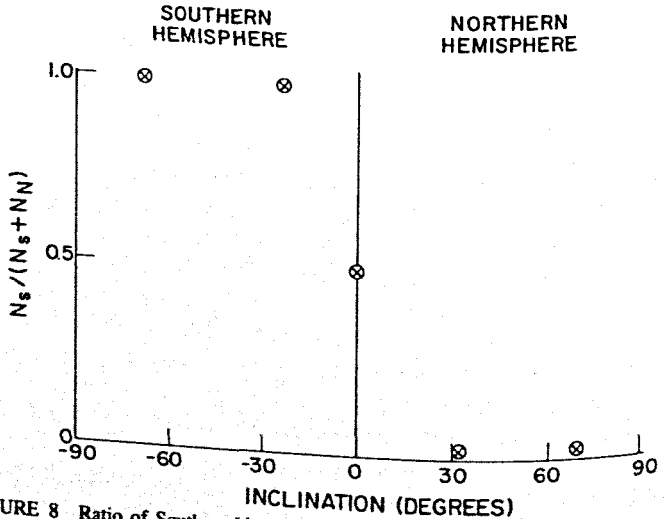


FIGURE 8 Ratio of South-seeking bacteria to total magnetotactic bacteria in natural environments, plotted as a function of the angle of inclination of the geomagnetic field.

roughly equal numbers.[32] Thus, the vertical component of the geomagnetic field selects the predominant cell polarity in natural environments, with downward directed motion advantageous for, and upward directed motion detrimental to survival of the organisms.[33] At the geomagnetic equator where motion is directed horizontally, both polarities benefit because horizontally directed motion reduces harmful upward migration.

The role of the vertical magnetic field component has also been confirmed in laboratory experiments. When a sediment sample from New England, initially containing North-seeking bacteria, is placed in a coil that produced a field of twice the magnitude and opposite sign to the ambient vertical field, the polarity of the bacteria in the sample is observed to invert over several weeks, that is over many bacterial generations.[28] If a sample is placed in a coil that cancels the vertical component of the ambient magnetic field, the population in the sample tends toward equal numbers of both polarities, again over many generations. Equal numbers of both polarities are also obtained when samples initially containing all North- or all South-seeking bacteria are placed in an enclosure that cancels the ambient magnetic field ($H < 0.01$ G).[32] Further experiments in null field by Blakemore and his students[34] confirm the role of oxygen. When samples with tight stoppers are placed in the zero field enclosure, bacteria of both polarities are ultimately found in the sediment and in the water column up to the surface. When the sample bottles are loosely stoppered, allowing diffusion of air, bacteria are found in the sediments but not in the water column.

Other possible advantages of magnetotaxis to bacteria involve rapid migration along magnetic field lines. This could be useful for population dispersal, as an escape response, or in outrunning chemical diffusion.[25] There are also consequences of magnetotaxis and $Fe_3O_4$ synthesis that may or may not be advantageous. Magnetic bacteria that are within 4 μm of each other will experience magnetic forces greater than the forces of Brownian motion. $Fe_3O_4$ synthesis also increases the density of the bacteria, helping them to stay down in the sediments even when they are not swimming, and may serve some metabolic functions as well.[34] Finally, magnetotactic bacteria live their lives and carry out all their cellular functions in a magnetic field of their own making which varies from over a thousand gauss at the surface of the particles to tens of gauss at the periphery of the cell.

## DISCUSSION

While the ability to synthesize $Fe_3O_4$ and construct magnetosomes is certainly genetically encoded, the polarity of the magnetosome chain cannot be encoded. If a bacterium that lacks magnetosomes starts to synthesize them *de novo* there is equal probability that, when the particles grow to permanent single domain size, the chain will magnetize with North-seeking pole forward or with South-seeking pole forward; a population of these bacteria will consist of 1:1 North-seekers and South-seekers. If however, the daughter cells inherit some of the parental magnetosomes during cell division, they will inherit the parental polarity (Figure 9). As they synthesize new magnetosomes at the ends of their inherited chains, the magnetic field produced by the existing particles will magnetize the new particles in the same direction. Thus North-seeking bacteria can produce North-seeking progeny and South-seeking bacteria can produce South-seeking progeny. However, there are mechanisms by which some progeny with the opposite polarity are produced in each generation. For example, if in the cell division process, some of the daughter cells inherit no parental magnetosomes, these cells will synthesize them *de novo* and about one-half of those cells will end up with the polarity opposite to that of the parents. So for example, in New England where North-seeking bacteria are found and predominate, some South-seekers are produced in each population division. Under normal circumstances, these South-seekers are unfavored by being directed upwards towards the surface when they are separated from the

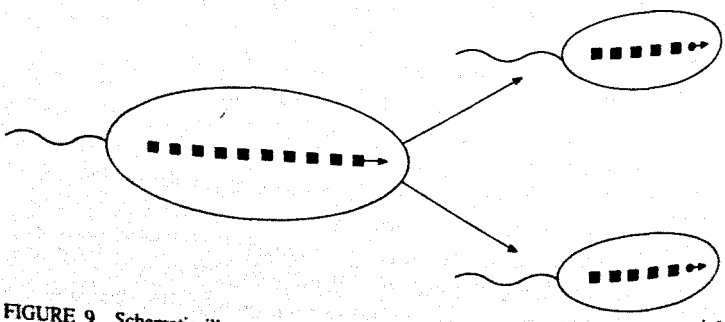

FIGURE 9 Schematic illustration of magnetosome inheritance hypothesis, illustrating how North-seeking cells produce predominantly North-seeking progeny. If one of the daughter cells receives no parental magnetosomes it has a 50% chance of becoming South-seeking.

sediments, and their total population remains low compared to the North-seeking population. However, when the vertical magnetic field is inverted, as in the experiment described above, these South-seekers are suddenly favored and their progeny eventually predominate as the previously favored North-seeking population declines in their newly unfavorable circumstances. When the vertical component is set equal to zero, neither polarity is favored and the population eventually equalizes. We can envision a similar process occurring in natural environments during reversals or excursions of the geomagnetic field.[35] During these processes the vertical component changes sign over thousands of years. This would be accompanied by a change in the predominant polarity of the magnetotactic bacterial population in that locale.

It is also interesting to consider the relationship between North and South-seeking bacteria. They are not mutants, since one can be produced from the other by magnetic means. Neither are they enantiomers or mirror image pairs. They can be described as ecophenotypes[36] but if we consider only their swimming directions and magnetic polarity (Figure 6) they can also be described as parity types. That is, they are converted by a parity transformation. In this transformation $x \rightarrow -x$, $y \rightarrow -y$ and $z \rightarrow -z$, reversing polar vectors but not axial vectors. As velocity direction is a polar vector and magnetic moment an axial vector, a parity transform operation (the magnetic pulse) essentially reverses the swimming direction but not the magnetic moment, transforming North-seekers into South-seekers and vice versa.

Finally, it is interesting to speculate on the evolution of the magnetotactic response. Oxygen toxicity or, in the period before the oxygenation of the atmosphere and the creation of the ozone layer, ultraviolet toxicity might have made it advantageous for the ancestors of modern magnetotactic bacteria to stay away from the water surface and in the sediments. If bacteria had precipitated higher density mineral produced for whatever reason, they would have increased their average density, that is, taken on ballast. Hydrous iron oxide minerals such as ferrihydrite and lepidocrocite are known to be precipitated by certain species of bacteria (the so-called iron bacteria) from iron ions available in the environment,[37] and hence are good candidates for the precipitation products of the hypothetical ancestors. However, the densities of the hydrous iron oxides are typically ~3.0. Magnetite with density 5.1 would be even more advantageous as ballast for organisms able to synthesize $Fe_3O_4$ by partial reduction and dehydration of the hydrous

iron oxides. After organisms could precipitate $Fe_3O_4$, we can imagine optimization of the magnetotactic response by natural selection. Note that the ballast argument applies to essentially nonmotile organisms because only for them will the vertical distribution be determined solely by gravitational and thermal forces. Motile organisms would require tactic responses to distinguish up from down. In order to function as a gravity transducer, a large mass of $Fe_3O_4$ would have to be situated forward in the bacterium with respect to the flagellum. However, for micron sized organisms $Fe_3O_4$ is several hundred times more efficient as a magnetic transducer than as a gravity transducer.[38]

If downward direction motion of a bacterial population by magnetotaxis is desirable, what is the minimum average moment or minimum amount of magnetite required? In general, the population will be effectively directed downward when the average orientation in the vertical direction is greater than the root mean squared deviation from the average orientation. In the Langevin theory this condition is satisfied when $\alpha(=MH/kT) \geq 2$. Thus at large inclinations, as in New England, a population with an average moment of approximately $1.6 \times 10^{-13}$ emu is sufficiently well oriented in the geomagnetic field of 0.5 G to be directed downward and not upward. This moment corresponds to about three 500-Å magnetite particles per cell.

## CONCLUSION

Magnetotactic bacteria are magnetic bacteria, synthesizing an intracytoplasmic $Fe_3O_4$ permanent dipole moment which functions as a biomagnetic compass. Recently, magnetotactic green algae of the genus *Chlamydomonas* have been discovered in sediments from brackish coastal lagoon in Rio de Janeiro, Brazil[39] and from a mangove swamp in Key Largo, Florida. Magnetotaxis in these eukaryotic microorganisms is similar to that in magnetotactic bacteria, that is, passive orientation of the cell by the torque exerted by the magnetic field on a permanent magnetic dipole moment in the cell. Algae from Brazil are South-seeking; algae from Florida are North-seeking. The magnetic moment of an alga was measured by cinematographically determining the swimming speed and the width of a U-turn following reversal of the magnetic field [Eq. (12)].[39] The moment $M \simeq 10^{-11}$ emu, about ten times larger than the typical bacterial moments. If the permanent magnetic material

in the algae is $Fe_3O_4$, there should be about 200 particles of 500 Å dimension in each cell. This is presently being investigated with electron microscopy.

Since the response time in passive magnetic orientation is roughly the cube of the radius divided by the magnetic moment [Eq. (10)], passive magnetotaxis is probably not a useful mechanism for organisms larger than about 10 microns radius. For larger organisms very large moments would be required to maintain rapid response times. However, other organisms including pigeons,[40] bees[41] and chitons[42,43] are known to contain $Fe_3O_4$,[44] and in some of these organisms $Fe_3O_4$ could conceivably function as the basis of a magnetic field sensing organ which would allow the use of the geomagnetic field for orientational and temporal cues.

**Acknowledgments**

I am pleased to acknowledge Richard P. Blakemore for continuing collaboration and critical commentary. I also thank C. P. Bean, J. Danon, D. M. S. Esquivel, S. J. Gould, H. Hartman, I. S. Jacobs, A. J. Kalmijn, H. Lins de Barros, H. Lowenstam, E. M. Purcell, C. Rosenblatt and F. F. Torres de Araujo for communications and discussions. This work was partially supported by the Office of Naval Research. The Francis Bitter National Magnet Laboratory is supported by the National Science Foundation.

RICHARD B. FRANKEL
*Francis Bitter National Magnet Laboratory,*
*Massachusetts Institute of Technology,*
*Cambridge, Massachusetts 02139*

**References**

1. C. Walcott, IEEE Trans. Magn. **MAG-16,** 1008 (1980).
2. J. L. Gould, Am. Sci. **68,** 256 (1980).
3. J. B. Phillips and K. Adler, in *Animal Migration, Navigation and Homing,* edited by K. Schmidt-Koenig and W. T. Keeton (Springer, Berlin, 1978), p. 325.
4. A. J. Kalmijn, Ref. 3, p. 345.
5. J. Mather and R. R. Baker, Nature **267,** 144 (1981).
6. R. R. Baker, Science **210,** 555 (1980).
7. J. L. Gould and K. P. Able, Science **212,** 1061 (1981).
8. R. P. Blakemore, Science **190,** 377 (1975).

9. A. J. Kalmijn and R. P. Blakemore, in *Animal Migration, Navigation and Homing*, edited by K. Schmidt-Koenig and W. T. Keeton (Springer, Berlin, 1978), p. 354.
10. D. B. Balkwill, D. Maratea and R. P. Blakemore, J. Bacteriol. **141,** 1399 (1980).
11. R. B. Frankel, R. P. Blakemore and R. S. Wolfe, Science **203,** 1355 (1979).
12. K. M. Towe and T. T. Moench, Earth Planet. Sci. Lett. **52,** 213 (1981).
13. R. P. Blakemore, D. Maratea and R. S. Wolfe, J. Bacteriol. **140,** 720 (1979).
14. For general discussions of the magnetism of ferrites see: B. Lax and K. J. Button, *Microwave Ferrites and Ferrimagnetics* (McGraw-Hill, New York, 1962); A. H. Morrish, *The Physical Principles of Magnetism* (Wiley, New York, 1968).
15. R. B. Butler and S. K. Banerjee, J. Geophys. Res. **80,** 4049 (1975).
16. C. P. Bean and J. D. Livingston, J. Appl. Phys. **30,** 1205 (1959).
17. I. S. Jacobs and C. P. Bean, Phys. Rev. **100,** 1060 (1955).
18. R. B. Frankel and R. P. Blakemore, J. Magn. Magn. Mater. **15–18,** 1562 (1980).
19. M. Holz and S. H. Chen, Biophys. J. **26,** 243 (1979).
20. R. P. Blakemore, A. J. Kalmijn and R. B. Frankel, unpublished.
21. B. D. Teague, M. K. Gilson and A. J. Kalmijn, Biol. Bull. **157,** 399 (1979).
22. A. J. Kalmijn, IEEE Trans. Magn. **MAG-17,** 1113 (1981).
23. E. M. Purcell, private communication.
24. C. P. Bean, private communication.
25. E. M. Purcell, Am. J. Phys. **45,** 3 (1977).
26. B. Berne and R. Pecora, *Dynamic Light Scattering* (Wiley, New York, 1976).
27. C. Rosenblatt, F. F. Torres de Araujo and R. B. Frankel, J. Appl. Phys., in press.
28. R. P. Blakemore, R. B. Frankel and A. J. Kalmijn, Nature **286,** 384 (1980).
29. C. R. Denham, R. P. Blakemore and R. B. Frankel, IEEE Trans. Magn. **MAG-16,** 1006 (1980).
30. T. T. Moench and W. A. Konetzka, Arch. Microbiol. **119,** 203 (1978).
31. J. L. Kirschvink, J. Exp. Biol. **86,** 345 (1980).
32. R. B. Frankel, R. P. Blakemore, F. F. Torres de Araujo, D.M.S. Esquivel, and J. Danon, Science **212,** 1269 (1981).
33. R. P. Blakemore and R. B. Frankel, Sci. Am. **245,** 58 (1981).
34. R. P. Blakemore, Ann. Rev. Microbiol. **36,** (1982).
35. A. Cox, Rev. Geophys. Space Sci. **13,** 35 (1975).
36. S. J. Gould, private communication.
37. M. P. Silverman and H. L. Ehrlich, Adv. Appl. Microbiol. **6,** 153 (1964).
38. R. B. Frankel, Eos **62,** 850 (1981).
39. H. G. P. Lins de Barros, D. M. S. Esquivel, J. Danon, L. de Oliveira and R. B. Frankel, Nature, submitted.
40. C. Walcott, J. L. Gould and J. L. Kirschvink, Science **205,** 1027 (1979).
41. J. L. Gould, J. L. Kirschvink and K. S. Deffeyes, Science **201,** 1026 (1978).
42. K. M. Towe and H. A. Lowenstam, J. Ultrastructure Res. **17,** 1 (1967).
43. J. L. Kirschvink and H. A. Lowenstam, Earth Planet. Sci. Lett. **44,** 193 (1979).
44. H. A. Lowenstam, Science **211,** 1126 (1981).